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Research paper

# Using environmental features to model highway crossing behavior of Canada lynx in the Southern Rocky Mountains

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## HIGHLIGHTS

- Lynx crossed two-lane paved highways an average of 0.6 times per day.
- Lynx crossed roads more at dusk and night, coincident with lower traffic volumes.
- Forest cover was predictive of lynx highway crossings at fine and landscape scales.
- Predictions from remotely-sensed covariates validate well with independent data.

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## ABSTRACT

Carnivores are particularly sensitive to reductions in population connectivity caused by human disturbance and habitat fragmentation. Permeability of transportation corridors to carnivore movements is central to species conservation given the large spatial extent of transportation networks and the high mobility of many carnivore species. We investigated the degree to which two-lane highways were permeable to movements of resident Canada lynx in the Southern Rocky Mountains based on highway crossings (n = 593) documented with GPS telemetry. All lynx crossed highways when present in home ranges at an average rate of 0.6 crossings per day. Lynx mostly crossed highways during the night and early dawn when traffic volumes were low. Five of 13 lynx crossed highways less frequently than expected when compared to random expectation, but even these individuals crossed highways frequently in parts of their home range. We developed fine- and landscape-scale resource selection function (RSF) models with field and remotely sensed data, respectively. At the fine scale, lynx selected crossings with low distances to vegetative cover and higher tree basal area; we found no support that topography or road infrastructure affected lynx crossing. At the landscape scale, lynx crossed highways in areas with high forest canopy cover in drainages on primarily north-facing aspects. The predicted crossing probabilities generated from the landscape-scale RSF model across western Colorado, USA, were successful in identifying known lynx crossing sites as documented with independent snow-tracking and road-mortality data. We discuss effective mitigation based on model results.



## 1. Introduction

Road distribution and density can have a significant impact on the connectivity of wildlife populations (Andrews, 1990; Forman & Alexander, 1998). Increased human activity, vehicle-related mortality, and behavioral avoidance of roads can all contribute to changes in movement, survival, and reproductive success of individuals and populations (Forman & Alexander, 1998; Ferreras, Aldama, Beltran, & Delibes, 1992; Trombulak & Frissell, 2000). Roads may also reduce gene flow for some species (Jackson & Fahrig, 2011; Riley et al., 2006). In particular, carnivores are susceptible to reduced population connectivity due to roads given their large home ranges, long-distance movements, and low recruitment rates

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(Noss, Quigley, Hornocker, Merrill, & Paquet, 1996; Woodroffe & Ginsberg, 2000).

Actions that promote highway permeability for carnivores require an empirical basis so that highway mitigation is most effective. Methods used to site animal-crossing structures and to identify animal crossing zones include expert opinion (Clevenger, Wierzchowski, Chruszcz, & Gunson, 2002), wildlife-vehicle collision patterns (Clevenger, Chruszcz, & Gunson, 2003; Malo, Suarez, & Diez, 2004), remote cameras (Cain, Tuovila, Hewitta, & Tewes, 2003), track surveys (Clevenger & Waltho, 2005; Grilo, Bissonette, & Santos-Reis, 2009), and telemetry (Dodd, Gagnon, Boe, & Schweinsburg, 2007; Tigas, Van Vuren, & Sauvajot, 2002). However, the use of actual crossing locations to determine attributes that carnivores select at highway crossings ensures that already limited funds are expended on conservation measures that truly enhance highway permeability and reduce carnivore mortality. Physical structures that increase permeability of highways to carnivores, such as underpasses and overpasses, must be placed in areas that are consistent with the species' resource-use (Clevenger & Waltho, 2000).

For many species, crossing zones and vehicle-related mortalities tend to be spatially clustered, an indication that animals may cross highways non-randomly in response to habitat or road characteristics (Malo et al., 2004; Neumann et al., 2012; Ramp, Caldwell, Edwards, Warton, & Croft, 2005). The types and spatial distribution of these characteristics vary by species, depending on life history and habitat preferences (Chetkiewicz & Boyce, 2009; Ramp, Wilson, & Croft, 2006). Vegetation characteristics tend to be important for many species. For instance, Seiler (2005) found that moose (*Alces alces*) and vehicle collisions were more likely to occur in areas with greater forest cover and proximity to forest edge. Clevenger et al. (2003) found that small mammal vehicle collisions tended to occur along roads near vegetative cover, and Finder, Roseberry, and Woolf (1999) showed that white-tail deer (*Odocoileus virginianus*) collisions were more likely in areas nearer to forest cover, gullies, or riparian zones. Lewis et al. (2011) modeled black bear (*Ursus americanus*) road-crossing probability and found that bears were more likely to cross in areas with less human development and greater forest cover. Thus, species-specific models that predict highway crossing zones should provide more accurate information on the likelihood of a given area to be used as a crossing, and therefore increase our ability to manage highway permeability and reduce direct vehicle-related mortality of rare carnivores.

The need for connectivity may be particularly important for reintroduced species at their range periphery, given low density and high degree of geographic isolation (Devineau, Shenk, Lukacs, & Kahn, 2010). Populations that are small and geographically isolated from their core range are generally vulnerable to local extinctions (Harrison, 1991; Lawton, 1993) that may be exacerbated by collision-mortality of dispersers and road avoidance (Forman et al., 2003). This concern is particularly acute for reintroduced populations of Canada lynx (*Lynx canadensis*) at their southern range periphery. Canada lynx are a medium-sized felid that generally occupy spatially distinct home ranges, but are also capable of long-distance exploratory or dispersal movements (Aubry, Koehler, & Squires, 2000; Squires & Oakleaf, 2005). Canada lynx are specialist predators of snowshoe hare (*Lepus americanus*) and are associated with moist, high-elevation spruce-fir forests in the Rocky Mountains of North America (McKelvey, Aubry, & Ortega, 2000). Vehicle collisions accounted for nearly half of mortalities for reintroduced lynx in the Adirondack Mountains, New York (McKelvey et al., 2000). Vehicle collision was also an important mortality factor for reintroduced lynx in Colorado (20% of mortalities; Devineau et al., 2010) and 45% of Eurasian lynx (*Lynx lynx*) mortalities in Germany (Kramer-Schadt, Revilla, & Wiegand, 2005).

Here we examine the road crossing characteristics of a reintroduced population of Canada lynx in the Southern Rocky Mountains of Colorado, USA. We first evaluated highway-crossing behavior of Canada lynx in terms of diel timing and road avoidance. We then evaluated the extent to which environmental variables at two spatial scales (fine scale and landscape scale) could be used to predict the probability of highway crossings by lynx. At lynx highway crossings, we quantified fine-scale environmental covariates in the field to evaluate crossings using variables not easily evaluated with remote sensing, such as forest structure and composition, presence of highway guard rails and barriers, and the distance that oncoming traffic was visible. Next, given that lynx are highly mobile (Devineau et al., 2010), our landscape-scale analysis evaluated if environmental heterogeneity quantified with remotely-sensed data could be used to predict highway crossings throughout western Colorado for region-wide planning. Given that lynx generally prefer spruce-fir forests with high horizontal cover (Fuller & Harrison, 2010; Koehler et al., 2008; Squires, DeCesare, Kolbe, & Ruggiero, 2010), we predicted that lynx at both fine and landscape scales would preferentially select forested crossing zones and generally avoid open habitat types.

## 2. Material and methods

### 2.1. Study area

Our study areas were in western Colorado, USA and included portions of the San Juan National Forest (37.6°N, 108.0°W) (referred to as SJNF hereafter) in Ouray, San Miguel, and Dolores counties, and the White River National Forest (39.5°N, 106.2°W) (referred to as WRNF hereafter), in Summit County (Fig. 1). The SJNF area occurred within the western San Juan Mountains and encompassed portions of the upper Animas, Dolores, and San Miguel River watersheds. The San Juan Mountain range was the core area in which the Colorado Division of Wildlife reintroduced lynx between 1999 and 2006 (Devineau et al., 2010). The SJNF included portions of two-lane U.S. Highway 550 and State Highway 145, with average daily traffic volumes between 2000 and 2500 vehicles per day (Colorado Department of Transportation, 2014). In the WRNF, the primary highways included Interstate 70 (I-70; 23,000 vehicles/day), a four-lane highway, and two-lane State Highway 91 (4000 vehicles/day; Colorado Department of Transportation, 2014).

Study areas were typical of the Southern Rockies with steep mountains and narrow valleys at elevations ranging approximately 2000–4300 m asl. Steep elevation gradients and high topographic variation across the study area produced a mosaic of conifer and aspen forests extending to alpine tundra, with herbaceous and shrub openings occurring as avalanche paths, meadows, and wetlands. Conifer-dominated forests, which provide most lynx habitat, occur between 2500 m to 3500 m asl in elevation and were composed primarily of Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*). Aspen (*Populus tremuloides*) and willow (*Salix* spp.) were common on disturbed slopes and intermixed with conifers in mid-seral stands, while Douglas fir (*Pseudotsuga menziesii*) occurred at low elevations. Lodgepole pine (*Pinus contorta*) dominated relatively drier forests on the WRNF but was largely absent from the SJNF. Winters were relatively long and cold; summers were drier but included monsoonal rain patterns that resulted in regular but brief afternoon precipitation. Maximum snow depth averaged 138 cm (range = 97–201 cm; Natural Resources Conservation Service, 2015), and snow generally persisted from November through May (low elevations) or June (high elevations and northerly aspects).

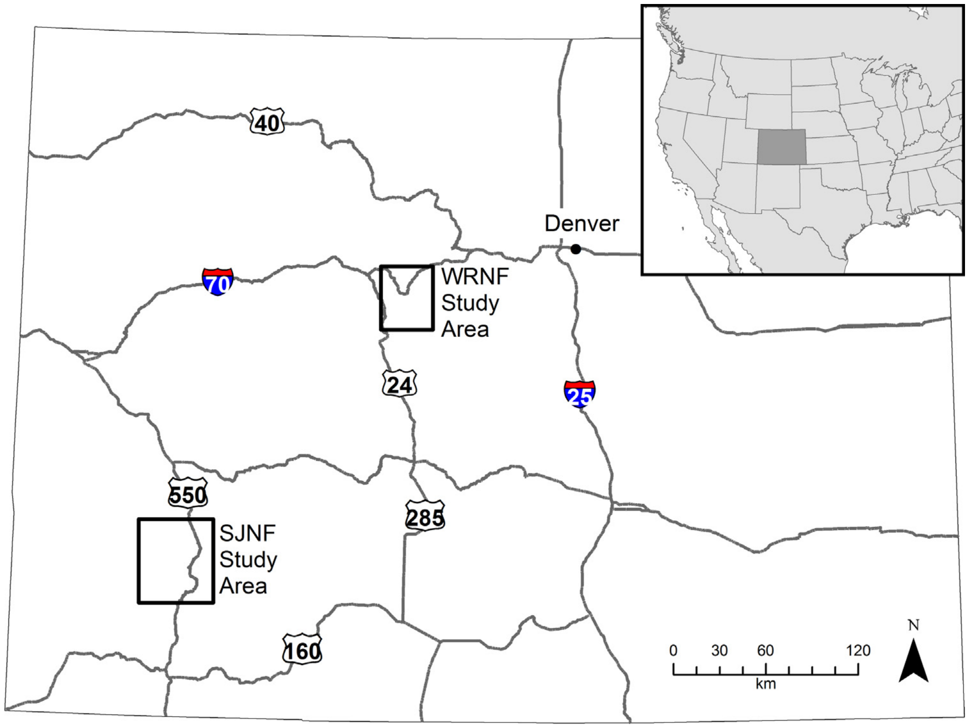



**Fig. 1.** Canada lynx study areas in western Colorado, USA including the White River National Forest (WRNF) and the San Juan National Forest (SJNF). Major highways in the area are indicated by gray lines; inset shows the location of Colorado in the United States.

### *2.2. Lynx capture and highway-crossing behavior*

During winters 2010–2012, we captured lynx in box traps according to Kolbe, Squires, and Parker (2003). Lynx were captured and handled under the guidelines in Animal Care and Use Permit CDOW-ACUC File#13-2009. We fitted captured lynx with global positioning system (GPS) collars (Sirtrack Ltd., Havelock North, New Zealand) programmed to collect locations every 20 or 30 min, from January to April. We programmed collars to automatically drop off between April and May. Using GPS-collar data, we defined lynx movement segments as straight-line vectors between consecutive GPS locations. We identified lynx crossing segments as movement segments intersecting highway centerlines (Laurian et al., 2008; Schwab & Zandbergen, 2011). We limited analyses to crossing segments with at least one lynx location within 200 m of a highway to ensure accuracy.

We investigated lynx avoidance of highways by quantifying movements within home ranges relative to simulated movements. We created home ranges using package 'adehabitatHR' (Calenge, 2006) in R (R Development Core Team, 2014) and calculated a utilization distribution for each lynx with a 90% kernel density estimate and reference bandwidth as the smoothing parameter (Worton, 1989). In each 90% home range, we compared the number of times that lynx actually crossed a highway to the number of random highway crossings simulated by correlated random walks (CRW; Kareiva & Shigesada, 1983). We used the Geospatial Modeling Environment (GME; Beyer, 2012) to generate 500 CRW simulations per lynx. Each CRW simulation started at the lynx capture location and drew from the observed distribution of movement segment lengths and turning angles to create an equal number of random movement segments within the home range. At each CRW iteration, we tallied the number of movement segments that crossed highways and had either the start or end point within 200 m of a highway, to be consistent with how lynx crossings were counted. We then compared the empirical frequency distribution of random crossing segments generated for each lynx to the observed number of highway crossing segments per lynx as a non-parametric bootstrap test of highway avoidance. We defined significant avoidance of highways to have occurred when the observed number of highway crossings was equal to or less than the bottom 5% of the simulated crossing segment distribution (Shepard, Kuhns, Dreslik, & Phillips, 2008).

Although lynx are active throughout diel periods (Kolbe & Squires, 2007; Olson, Squires, DeCesare, & Kolbe, 2011), we expected most highway crossings would occur at night or during twilight periods when traffic volumes were low (Colorado Department of Transportation, 2014). We defined the time of highway crossing as the midpoint between the start and end times of lynx crossing movements. We categorized crossing times into four time periods: (1) dawn (2 h; sunrise ± 1 h), (2) day (10 h; sunrise + 1 h to sunset − 1 h), (3) dusk (2 h; sunset ± 1 h), and (4) night (10 h; sunset + 1 h to sunrise − 1 h); daily sunrise and sunset times were obtained from the National Oceanic and Atmospheric Earth Systems Research Laboratory (Cornwall, Horiuchi, & Lehman, 2015). We tallied the number of crossing segments within each time period for each lynx and then used a Poisson generalized linear mixed model to fit the number of crossings as a function of time period. We included time period as a fixed effect, individual lynx as a random intercept, and an offset term of log(time period hours) to account for differences in the length of each time period. We further qualitatively examined whether lynx crossed highways during times when they were most active by plotting the temporal pattern of lynx highway crossings relative to the temporal pattern of active lynx movement segments. Active movement segments were defined as those longer than the spatial error of stationary collars (92.5 m; Squires et al., 2013); segments shorter than this distance were considered to be resting or stationary.

### *2.3. Modeling resource selection*

We developed resource selection functions (RSFs) at a fine (field-collected variables) and a landscape (remotely-sensed variables) scale to predict highway crossing probability by lynx (Manly, McDonald, Thomas, McDonald, & Erickson, 2002). We restricted our model-fitting to data from two-lane paved highways because of their prevalence in lynx home ranges; however, we did apply the model predictions (see *Model Validation* section) to I-70, the only four-lane highway in lynx habitat in western Colorado. We also provide anecdotal observations of lynx crossing I-70 due to the central role that this high-volume, four-lane highway could have on lynx population connectivity. At fine and landscape scales, we used the glmer function in package 'lme4' (Bates, Maechler, Bolker, & Walker, 2014) in R to build RSF models using mixed-effects logistic regression, and accounted for differences in crossing behavior of individual lynx with a random intercept for individual. Predictor covariates were standardized by subtracting the mean and dividing by the standard deviation to facilitate comparison between variables measured at different scales. We developed plausible *a priori* multivariate candidate models (Appendix A) with covariates that were more informative than the null model in a univariate sense based on Akaike's Information Criterion (AIC; Burnham & Anderson, 2002). We excluded covariates with high collinearity ($|r| > 0.6$); if correlated, we retained the variable that was most biologically meaningful and available to managers. We estimated logistic regression models describing the probability of lynx highway crossing as:

$$\hat{w} = \exp\left(\beta_0 + \beta_1 x_1 + \ldots + \beta_n x_n\right) / \left(1 + \exp\left(\beta_0 + \beta_1 x_1 + \ldots + \beta_n x_n\right)\right) \quad (1)$$

where $\hat{w}$ is the probability of selection as a function of $x_n$ covariates, $\beta_n$ are the parameter coefficients, and $\beta_0$ is the intercept (Manly et al., 2002). We evaluated candidate models using AIC and identified top models as those within 4 ΔAIC of the best performing model that did not contain uninformative parameters (Arnold, 2010; Burnham & Anderson, 2002).

For fine-scale resource-use modeling, we quantified predictor covariates in the field at lynx highway crossings. We buffered used points by 100 m then selected available points from outside the buffers. This ensured that used and available points were non-overlapping to reduce the potential of used crossings being also considered as available (sample contamination; Johnson, Nielsen, Merrill, McDonald, & Boyce, 2006; Keating & Cherry, 2004). We randomly selected 15 actual crossing locations per lynx and 15 "crossings" randomly available in each lynx home range. For three lynx with <15 total highway crossings, we sampled all used crossing points regardless of overlap. We fit 13 multivariate candidate models (see Appendix A).

At the landscape scale, we evaluated lynx highway crossing behavior by comparing used lynx crossings ($n = 593$) to available crossing locations ($n = 4331$) distributed across highways in western Colorado. Since a large available sample is required to minimize bias in RSF models (Hooten, Hanks, Johnson, & Alldredge, 2013; Northrup, Hooten, Anderson, & Wittemyer, 2013), and to allow prediction across all highways in western Colorado within the elevation zone of lynx, we sampled available crossing points systematically spaced 1 km apart along all highways within the elevation zone used by lynx in our sample (2000–4183 m asl). We considered 29 multivariate candidate models (see Appendix A). Our mixed model framework required an available sample specific to each individual lynx; however, since our available landscape was common to all lynx, we used a bootstrap procedure to refit the model with a different random sample of all systematic points to verify model performance. We performed 1000 bootstrap iterations that randomly sampled each lynx's used and all available crossing points with replacement and fitted all 28 candidate models at each iteration. We used AIC values for model selection, and verified this using the number of times each model was ranked best across bootstrap iterations. We then spatially extrapolated our best-performing model to predict probability of crossing along major highways in western Colorado above 2000 m asl elevation.

### *2.4. Predictor covariates*

We quantified fine-scale vegetation covariates at crossing points with eight plots aligned in an "X" configuration (Appendix B1; Fig. 2). At each vegetation plot, we quantified tree basal area with a 10-factor prism and recorded diameter at breast height (DBH) by species. We also measured vegetative horizontal cover in each cardinal direction using a cover-board viewed at 10 m away, consistent with Squires et al. (2010). We measured distance to vegetative cover as the shortest distance to continuous vegetation greater than 2 m tall and in patches >25 m$^2$. We measured roadside covariates at three points to account for the spatial uncertainty of crossing locations (Appendix B1; Fig. 2). We quantified the slope of approaches to highways at 10 m perpendicular to the road with a clinometer. We used a rangefinder to measure the length of highway visible to a crossing animal, defined as the line-of-sight distance of continuous pavement in both directions. Given that highway structures can have physical or visual impact on wildlife crossings (Gunson, Mountrakis, & Quackenbush, 2011), we mapped the locations of physical barriers (e.g., guard rails, jersey barriers, vertical cliffs). We calculated the mean and standard deviation for all variables across all eight vegetation or three roadside plots at each crossing point.

At the landscape scale, we used remotely-sensed topographic and vegetation data (Appendix B2) at two spatial scales (200 m and 500 m radii circular moving windows) that we selected arbitrarily to capture the environment associated with highways. We selected landscape-scale covariates that best represented important variables associated with crossings identified during fine scale sampling and those that we thought were most biologically meaningful for landscape-level modeling. Topographic variables including slope, aspect, and terrain roughness were obtained from a 10 m digital elevation model (DEM; Gesch, 2007). Terrain roughness was calculated from the standard deviation of elevation values (Wilson & Gallant 2000). We calculated an index of "northness" using the percentage of cells in a 200 m or 500 m neighborhood with slope >10% and northerly aspects (>270° and <90°). Topographic position index (TPI), a measure of terrain concavity or convexity (Jenness, 2006), was calculated at a 1000 m scale, in addition to 200 and 500 m; the 1000 m radii plot was added to better characterize drainages in mountainous topography. Euclidian distance to hydrologic features was determined using the National Hydrography Dataset (NHD; United States Geological Survey, 2013). We obtained six 30 m resolution Landsat 5 Thematic Mapper (http://earthexplorer.usgs.gov/) scenes dated 8 June to 24 June 2011, each with less than 1% cloud cover. From these images, we derived the Normalized Difference Vegetation Index (NDVI; Jensen, 2005), an index of vegetation biomass, and performed tasseled cap transformations (Crist & Cicone, 1984), which created variables that index soil reflectivity (brightness), vegetation presence (greenness), and soil or surface moisture (wetness). We calculated the mean and standard deviation of NDVI, Brightness, Greenness, and Wetness. Finally, we evaluated forest structure based on a 30 m LANDFIRE v. 1.2.0 (Rollins, 2009) layer of canopy cover.

### *2.5. Model validation*

We evaluated our best fine-scale model using four-fold cross validation (Boyce, Vernier, Nielsen, & Schmiegelow, 2002). We randomly divided all used locations into four groups, sequentially withheld each group, fit the model on the remaining three groups, and used the model to predict the outcome of the withheld group according to Boyce et al. (2002). This method

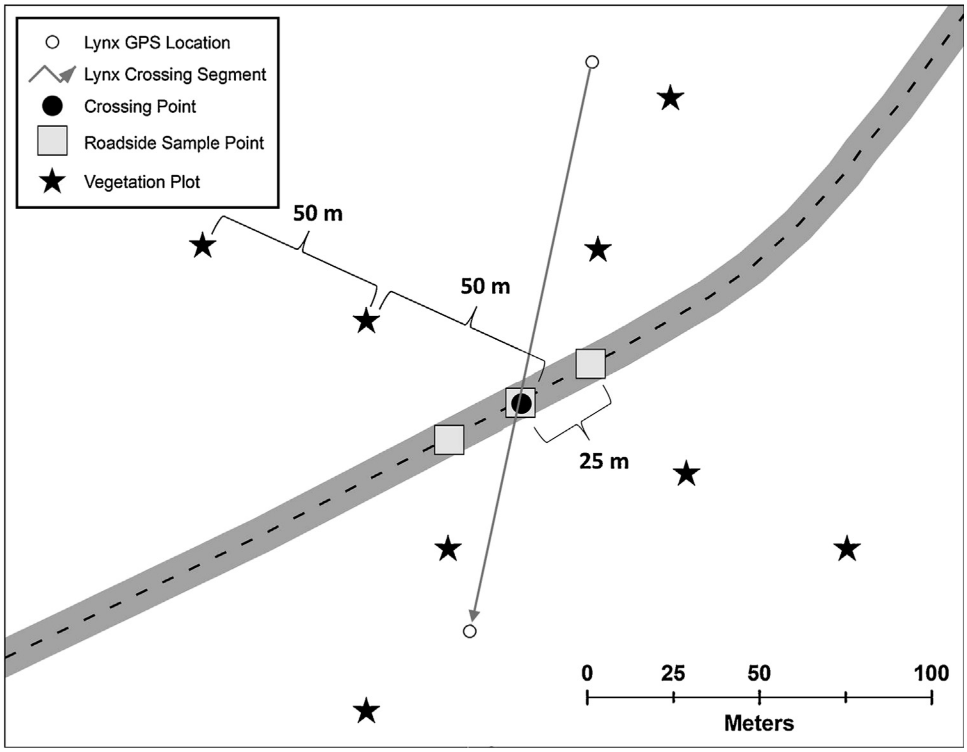



**Fig. 2.** Configuration of fine-scale vegetation plots at lynx highway crossings in western Colorado; eight plots in an "X" configuration were sampled. Three roadside sample points were spaced across putative crossing zones to quantify roadside characteristics.

should generate a high Spearman's rank correlation coefficient ($r_s$) between predictions from the withheld sample and the bin numbers generated from the entire dataset if the model is predicting the relative probability of road crossings given the range of probabilities over the entire area sampled (Boyce et al., 2002).

We evaluated the landscape-scale RSF model using two methods. First, we conducted a 10-fold cross validation according to Boyce et al. (2002), similar to the fine scale. Second, we used an independent dataset of lynx highway crossings in Colorado that consisted of winter lynx back-tracks from 2000 to 2009 ($n = 117$; Colorado Parks and Wildlife, unpublished data) and lynx highway mortalities from collisions with vehicles 1999–2015 ($n = 11$; Colorado Parks and Wildlife, unpublished data). We believed these independent data provided our best evaluation of model performance that mimicked actual field application. We extracted the RSF predicted probability value at each independent crossing location using our landscape-scale model; higher crossing probabilities indicated better predictive performance.

## 3. Results

We collected an average of 4810 GPS locations (SD = 2415, range: 752–8300) on each of 14 lynx (7 M, 7 F). Data collection ranged between 27 Jan and 17 Jun (Appendix C). Home ranges of all but one lynx were bisected by 4.0–52.9 km of two-lane highway ($\bar{x} = 18.7$ km, SD = 14.8). We documented 735 total lynx highway crossings; 88 of these were lower quality crossings (GPS locations >200 m off the highway and/or >40 min between locations) that were eliminated from further analysis. We used 11 of 13 lynx to model resource selection at 593 crossings; data from two lynx were not available for resource-use modeling due to late collar drop-offs. Elevation of lynx crossings averaged 3041 m (SD = 134 m, range: 2778–3451).

### 3.1. Highway crossing behavior

Lynx crossed highways more frequently during dusk and night than during dawn and day ($\beta_{dawn} = -0.17$, SE = 0.13, $p = 0.18$; $\beta_{dusk} = 0.76$, SE = 0.09, $p < 0.001$, $\beta_{night} = 1.31$, SE = 0.05, $p < 0.001$). Lynx crossed highways at increased frequency after sunset until 0100 h; crossing frequency remained relatively high until sunrise, after which it declined (Fig. 3). Lynx crossed highways during all hours, but crossings were 1.85 times more frequent during night ($n = 393$) than day ($n = 212$). Also, observed diel pattern of lynx highway crossings appeared to deviate from the general pattern of lynx activity (Fig. 3). For example, lynx movement activity generally decreased from sunset (1800 h) to 2400 h, while the frequency at which lynx crossed highways increased during this period.

Lynx crossed two-lane highways an average of 0.6 times per day (SD = 0.4, range: 0.2–1.4; Appendix C). The mean number of highway crossings per lynx was 50 (SD = 45.4; range: 6–148) compared to CRW paths that crossed an average of 90 times (SD = 60.0; range: 20–221; Appendix C). Correlated random walk simulations suggested that 5 (3 F, 2 M) of 13 lynx crossed highways significantly less than expected ($p < 0.05$) whereas 8 lynx exhibited no highway avoidance ($0.07 < p < 0.52$; Appendix C); all lynx with highways in their home ranges crossed more than once (Fig. 4).

Three of 5 lynx with adjacent home ranges crossed the four-lane interstate I-70 on 25 occasions. These crossings provided important anecdotal observations of behavior associated with crossing a high traffic volume highway, but the number of observations was insufficient for statistical evaluation with a resource selection function. These lynx mostly crossed I-70 near first- and second-order stream tributaries where eastbound interstate lanes were elevated by bridges 75–100 m long and 15–25 m in height with continuous tall woody vegetation underneath. The highway median between east and west-bound traffic in these areas was approximately 150–200 m wide and included patches of forest cover. Although traffic averaged approximately 1200 vehicles/hr during

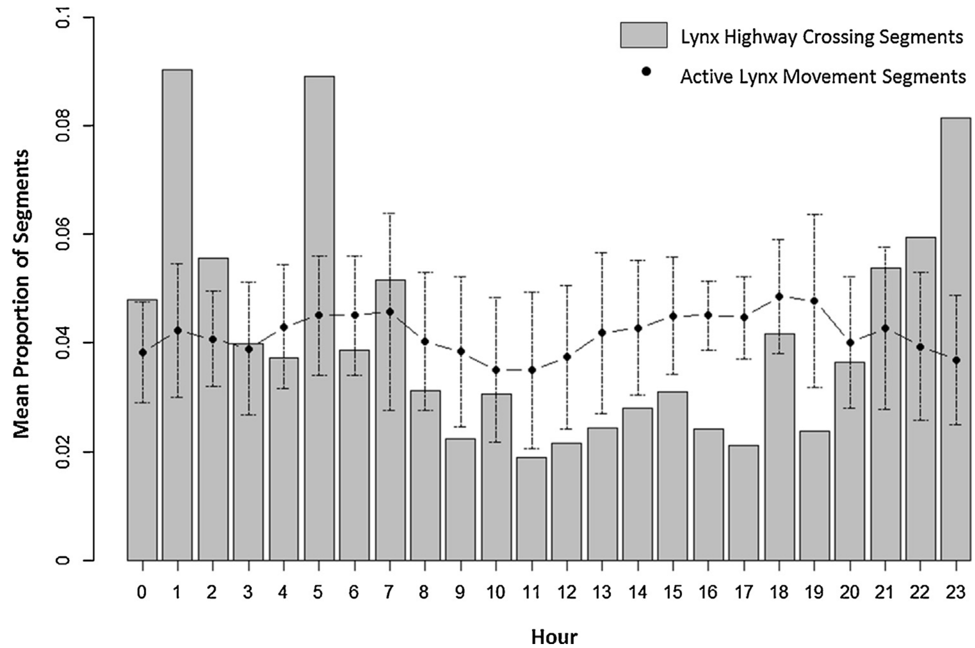



**Fig. 3.** Proportion of lynx GPS movement segments that cross highways (gray bars) each hour, versus proportion of all active movement segments (black circles +/−standard deviation) per hour for Canada lynx (N = 13) in western Colorado.

the day, volume was reduced to <200 vehicles/hr between 0100 h and 0500 h (Colorado Department of Transportation, 2014). Seven of 25 crossings occurred during this 0100–0500 h period of low traffic, while 9 crossings occurred during other dark hours. Snow tracking data from an independent data set of lynx not included in this study indicated that lynx successfully crossed I-70 on at least three occasions, all about 30 km east of where collared individuals crossed. Large elevated bridges over natural habitat were absent from this stretch of the interstate and these crossings occurred at grade, over the road surface. However, two lynx in the independent data set were killed while attempting to cross at grade in this area and two were killed attempting to cross at grade near the underpasses described above. It is unclear whether those killed while attempting to cross I-70 had crossed successfully in previous attempts.

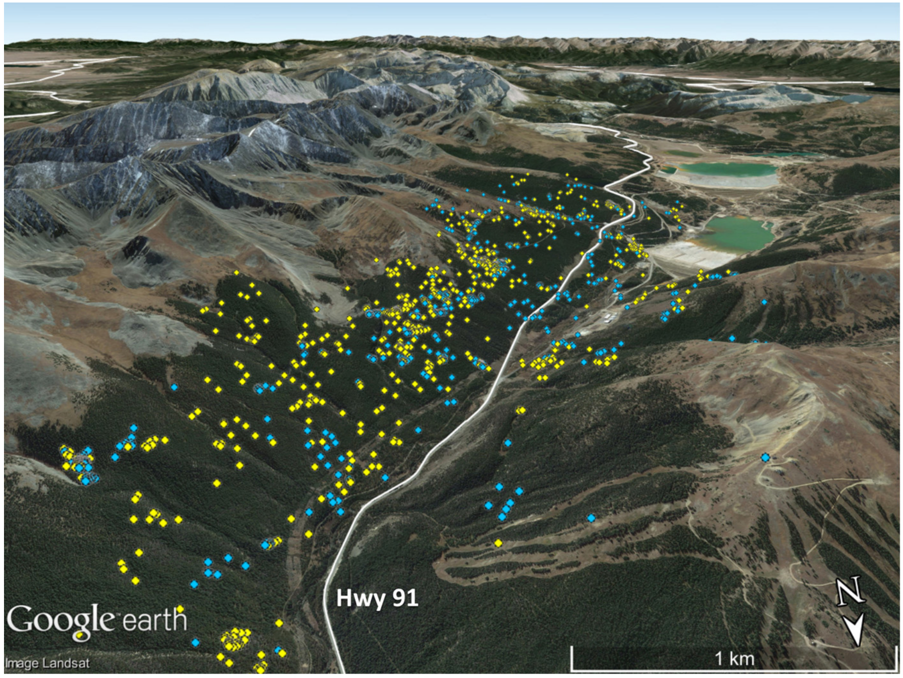
### 3.2. RSF models at multiple scales

At the fine scale, lynx were most influenced by vegetation characteristics. No topographic or highway infrastructure covariates performed better than null models in univariate analyses, so they were not considered further. Based on final multivariate models, lynx selected highway crossing zones that were closer to vegetative cover (MaxDistCover) and had greater mean basal area (AvgBasalArea) (Table 1). There were five models within four ΔAIC; following Arnold (2010), we considered models that differed by one extra parameter but were within two AIC of the top-performing model to contain uninformative terms. Thus, only MaxDistCover and AvgBasalArea were meaningful predictors of lynx crossings, although AvgBasalArea was only weakly predictive, as its 95% confidence interval slightly overlapped zero (Table 3). This suggested that lynx were most sensitive to the amount of forest and other vegetative cover along roads when selecting highway crossings. The mean MaxDistCover for used lynx crossings was 17.8 m (SD = 16.3 m), compared to 29.8 m (SD = 34.3 m) for available highway crossings. For every 1 m increase in distance to cover, the odds of highway crossing declined approximately 1.9%. Lynx also tended to select crossing zones with higher tree density compared to random: trees basal area was 78.3 $m^2$/ha (SD = 31.3 $m^2$/ha) at crossings compared to 59.5 $m^2$/ha (SD = 31.3 $m^2$/ha) at available locations. Mean horizontal cover and the proportion of spruce and fir trees at a crossing appeared among the top models but did not contribute to model performance. Lynx appeared insensitive to roadside slope, the presence of barriers, or line-of-sight distances when selecting highway crossing locations.

At the landscape scale, lynx selected crossings in areas of high forest canopy cover within the surrounding 500 m (LfCanCvr_500), concave topographic positions relative to the surrounding 1000 m (TPI_1000), and predominately northerly aspects within 200 m of the highway (PctNorth_200; Table 2). This top multivariate model ranked best in 57% of bootstrap iterations and was four times more likely than the next candidate model to explain the probability of where lynx crossed highways (Table 2). The second best performing multivariate model ranked best in 42% of bootstrap iterations and included canopy cover within the surrounding 500 m (LfCanCvr_500) and the standard deviation of brightness within the surrounding 500 m (StdBrt_500). All four predictors were strong with 95% confidence intervals that did not overlap zero (Table 3). We averaged predictions from the top 2 multivariate models (<4 ΔAIC) to produce a statewide RSF surface of potential lynx crossing zones along 4359 km of highways (i.e., those above 2000 m elevation) in western Colorado (Fig. 5). Model results suggest that 80% of highways within the elevation zone of lynx habitat in Colorado had less than a 50% chance of being used by lynx for crossings. In contrast, high probability crossing areas were relatively few and were concentrated in areas of high forest cover on north-facing slopes (Fig. 6).

### 3.3. Model validation

Cross-validation of the fine- and landscape-scale models indicated good model fit. A four-fold cross-validation of the best performing fine-scale RSF model had a Spearman correlation coefficient of $|r_s| = 0.94$. The 10-fold cross-validation for the landscape-scale averaged model yielded a Spearman correlation coefficient of 0.95. The independent data that we used for the landscape model validation consisted of 117 snow tracks of lynx crossing highways and 11 road-killed lynx mortalities. These inde-



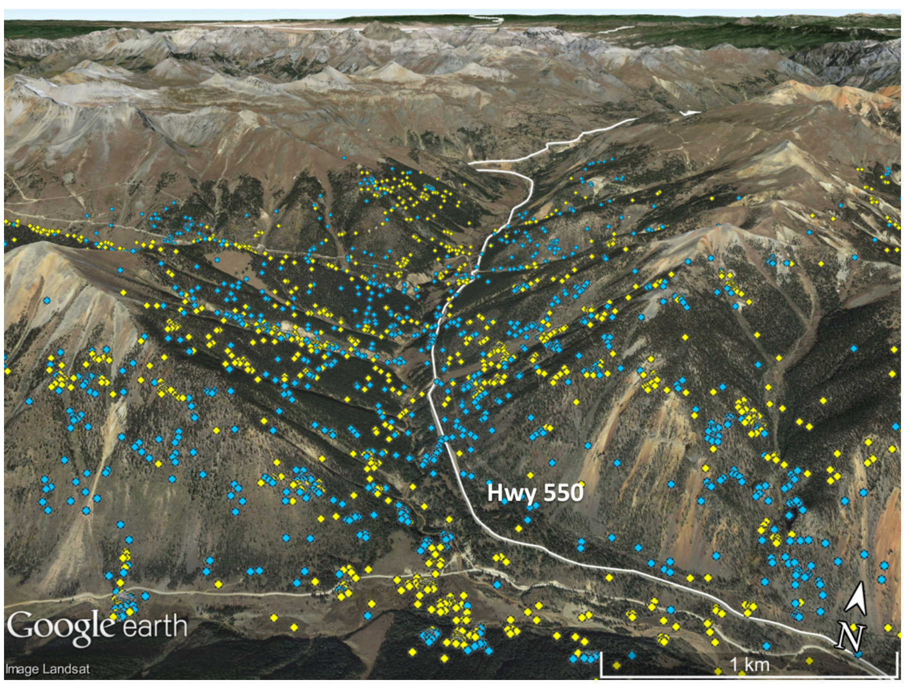




**Fig. 4.** Examples that illustrate most avoidance (top) and least avoidance (bottom) of 2-lane highways by Canada lynx based on GPS locations, western Colorado. Night locations (20:00 h–06:00 h) are shown in blue, while day locations (07:00 h–19:00 h) are shown in yellow. Even the individual exhibiting most highway avoidance (top) frequently used habitats immediately adjacent to the road. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

**Table 1**
Model selection results for fine-scale mixed-effects logistic regression models predicting Canada lynx highway crossings in western Colorado. The number of fixed effect parameters (K), AIC score, ΔAIC, AIC weight, and log-likelihood (LL) are given. Model variables include maximum distance to cover (MaxDistCover), mean basal area (AvgBasalArea), mean horizontal cover (AvgHorizCover), and the proportion of spruce and fir trees (PropSF). Only the 5 best performing models plus the null are reported.

| | Model | K | AIC | ΔAIC | AICwt | LL |
|---|---|---|---|---|---|---|
| 1 | MaxDistCover + AvgBasalArea | 4 | 409.79 | 0.00 | 0.36 | −200.90 |
| 2 | MaxDistCover | 3 | 411.23 | 1.43 | 0.18 | −202.62 |
| 3 | MaxDistCover + AvgBasalArea + AvgHorizCover | 5 | 411.29 | 1.50 | 0.17 | −200.65 |
| 4 | MaxDistCover + AvgBasalArea + PropSF | 5 | 411.76 | 1.97 | 0.13 | −200.88 |
| 5 | MaxDistCover + AvgBasalArea + AvgHorizCover + PropSF | 6 | 413.23 | 3.43 | 0.06 | −200.62 |
| 6 | NULL | 2 | 424.77 | 14.84 | 0.00 | −210.38 |

**Table 2**
Model selection results for landscape-scale mixed-effects resource selection models predicting Canada lynx highway crossings in western Colorado, giving the number of fixed effect parameters (K), AIC score, ΔAIC, AIC weight, log-likelihood (LL), and proportion of bootstrap iterations each model was ranked best (Prop Best). Variables included in the top models were mean percent canopy cover (LfCanCvr_500), topographic position index, percentage of area composed of north-facing aspects, standard deviation of brightness (StdBrt_500), and mean wetness (MeanWet_200). The number after each covariate denotes the size of the radius at which each covariate was calculated. Only the 5 best performing models plus the null are reported.

| | Model | K | AIC | ΔAIC | AICwt | LL | Prop Best |
|---|---|---|---|---|---|---|---|
| 1 | LfCanCvr_500 + TPI_1000 + PctNorth_200 | 5 | 828.03 | 0.00 | 0.80 | −409.01 | 0.57 |
| 2 | LfCanCvr_500 + StdBrt_500 | 4 | 830.80 | 2.78 | 0.20 | −411.40 | 0.42 |
| 3 | LfCanCvr_500 + MeanWet_200 + TPI_1000 | 5 | 839.22 | 11.19 | 0.00 | −414.61 | 0.01 |
| 4 | LfCanCvr_500 + TPI_1000 | 4 | 851.11 | 23.08 | 0.00 | −421.56 | 0 |
| 5 | LfCanCvr_500 + MeanWet_200 + PctNorth_200 | 5 | 868.10 | 40.07 | 0.00 | −429.05 | 0 |
| 6 | Null | 2 | 1510.81 | 682.79 | 0 | −753.41 | 0 |

**Table 3**
Model coefficients, with 95% confidence intervals, of covariates in top performing models within 4 ΔAIC used to predict Canada lynx highway crossings at two spatial scales (fine and landscape) in western Colorado. Model numbers correspond to Tables 1 and 2. Covariates included are maximum distance to cover (MaxDistCover), mean basal area (AvgBasalArea), mean percent canopy cover (LfCanCvr), topographic position index (TPI), percentage of an area composed of north-facing aspects (PctNorth), and the standard deviation of brightness (StdBrt). Numbers after the landscape scale model covariates indicate the size of the radius at which each covariate was calculated.

| Scale | Model | Variable | Coefficient | Lower 95% CI | Upper 95% CI |
|---|---|---|---|---|---|
| Fine Scale Models | Model 1 | MaxDistCover | −0.44 | −0.80 | −0.12 |
| | | AvgBasalArea | 0.24 | −0.01 | 0.51 |
| | Model 2 | MaxDistCover | −0.57 | −0.91 | −0.27 |
| Landscape Scale Models | Model 1 | LfCanCvr_500 | 1.82 | 1.66 | 2.01 |
| | | TPI_1000 | −0.56 | −0.68 | −0.45 |
| | | PctNorth_200 | 0.38 | 0.28 | 0.48 |
| | Model 2 | LfCanCvr_500 | 2.38 | 0.86 | 1.05 |
| | | StdBrt_500 | 0.86 | 0.67 | 1.05 |

pendent lynx crossings had a predicted average RSF value of 0.75 (range 0.15–0.98; SD = 0.18) from the landscape-scale RSF model (Fig. 6). Additionally, the predicted RSF values associated with all independent lynx crossings were largely between 0.6 and 0.8, with only 7% of independent data associated with modeled values less than 0.5 (Fig. 6). In contrast, the distribution of RSF values at all available locations across Colorado was largely between 0 and 0.1, with 78.82% of predicted probabilities less than 0.5. This suggested the landscape model was effective at predicting the actual areas that lynx would use when crossing highways.

## 4. Discussion

Canada lynx in the Southern Rocky Mountains of western Colorado crossed 2-lane highways (traffic volumes of 2000–4000 vehicles/day) approximately every other day. We found that most lynx (8 of 13) did not appear to avoid crossing roads, likely due to the habitat configuration of lynx home ranges in our study area. Lynx whose home ranges included extensive sections of highways lived in close proximity to them and crossed frequently. Lynx mitigated the risk of increased highway exposure by crossing roads at greater frequency during dusk and night, when traffic volume was lower. Our resource selection models were successful at predicting the probability of lynx crossing given fine- and landscape-scale environmental characteristics. At both spatial scales, lynx were more likely to cross highways in areas with greater vegetative cover, while at the landscape scale, lynx also preferred north-facing slopes and areas of topographical concavity, such as river drainages.

Despite the fact that all lynx crossed highways, we found that 5 of 13 individuals (39%) exhibited some degree of road avoidance behavior as defined by crossing significantly less than CRW simulations. Other studies have documented highway-avoidance behavior by lynx (Apps, 2000; Squires et al., 2013), although the lynx in our study that exhibited road avoidance behavior still frequently crossed roads in some regions of their home range, depending on forest vegetation near crossing zones (Fig. 4). Lynx reintroduced to the Southern Rocky Mountains occupied habitat in high-elevation mountain valleys that were bounded at upper elevations by open rock and tundra. Given the mountainous topography, two-lane highways in western Colorado were present in valley bottoms with vegetation too sparse for lynx, while other sections were high on mountain passes in good lynx habitat. We acknowledge that reintroduced lynx may exhibit different crossing behavior than native populations. However, of the 13 individuals in our study, five were born in the Southern Rockies, and the remaining eight were resident in the Southern Rocky Mountains for more than 5 years and had established home ranges. Thus, we believe our results reflected behaviors of established individuals and were not uninformed movements of naïve individuals in a new environment.

One way that lynx accommodated vehicle-related disturbance was to cross highways more frequently at night when traffic volumes were relatively low. The proclivity for lynx to cross highways at night was similar to other wide-ranging felids such as bobcat (*Lynx rufus*; Cain et al., 2003) and European wildcat (*Felis silvestris*; Klar, Herrmann, & Kramer-Schadt., 2009), as well as other taxa such as grizzly bears (*Ursus arctos*; Waller & Servheen, 2005) and elk (*Cervus elaphus*; Gagnon, Theimer, Dodd, Boe, & Schweinsburg, 2007). Tigas et al. (2002) reported that bobcats and coyote (*Canis latrans*) tended to utilize areas with high human activity more often at night. Nighttime traffic volumes on highways in western Colorado were generally <5% of peak early-afternoon volumes of 200–400 vehicles per hour (Colorado Department of Transportation, 2014). We assumed that increased crossings at night were an avoidance behavior to vehicle-related disturbance because lynx were generally active across all diel periods (Fig. 3). The tendency of lynx to preferentially traverse highways during periods of low traffic volume may also reduce the risk of vehicle-related mortality (Neumann et al., 2012). For example, Waller and Servheen (2005) demonstrated that grizzly bears experience lower risk in crossing highways at night compared to peak traffic volumes.

At a fine scale, lynx crossed highways in close proximity to vegetative cover, similar to several other large mammal species (Clevenger & Waltho, 2005). Vegetative cover was primarily provided by conifers in stands with higher basal area compared to randomly available along highways. We assume that road-side vegetation provided security cover and that higher horizontal

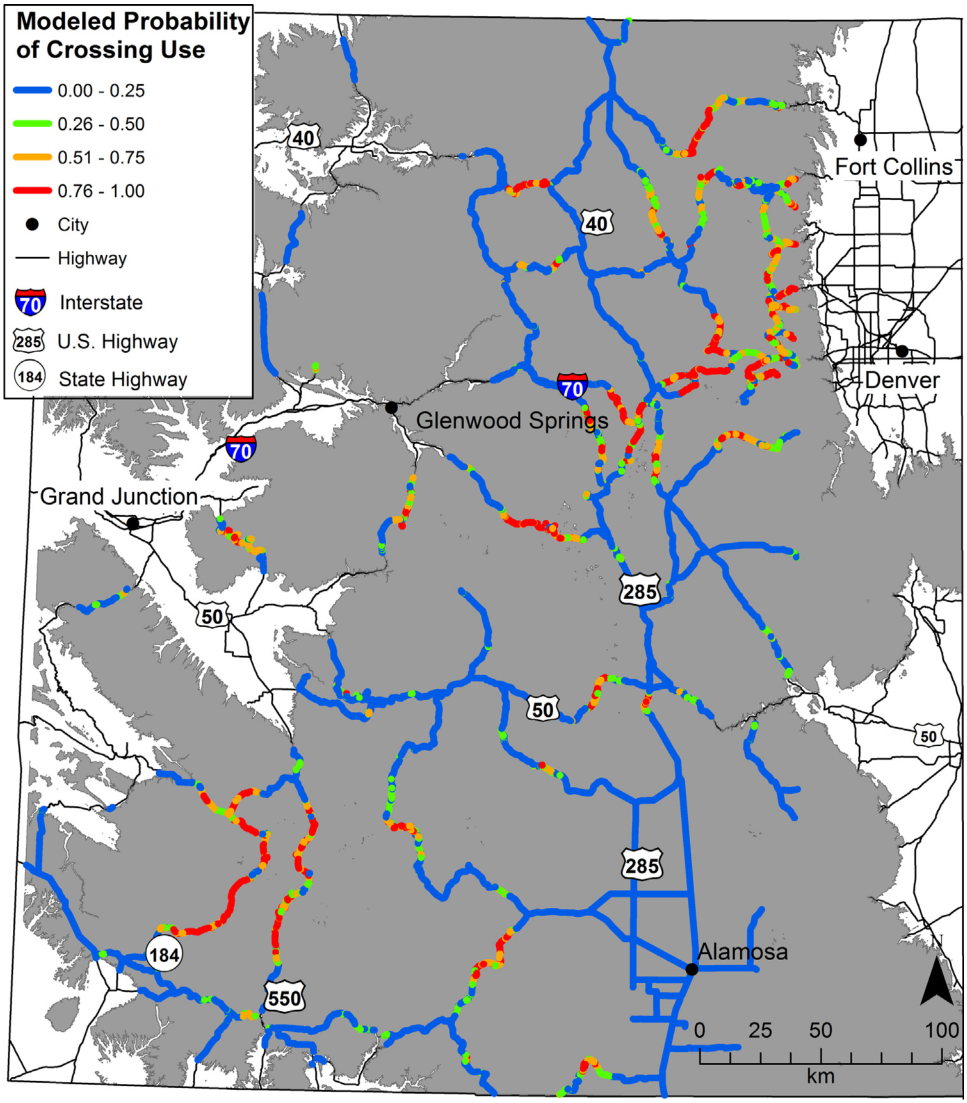



**Fig. 5.** Resource selection probability surface predicting Canada lynx crossings of highways (gray area indicates >2000 m elevation) at a landscape scale across western Colorado.

cover could support greater snowshoe hare densities (Fuller & Harrison, 2010; Hodges, 2000; Squires et al., 2010). Consistent with fine-scale results, lynx at the landscape scale selected north-facing crossings in areas of high forest canopy cover primarily in drainage bottoms. The landscape-scale model we developed generally agreed with other studies of wildlife highway crossings that identified important crossing areas near drainages with forest cover (Clevenger et al., 2003; Grilo et al., 2009). Our landscape model based on remotely-sensed environmental covariates provides a useful management tool to predict areas of high permeability to lynx movement, as evidenced by performance with independent crossing data. The fact that independent lynx crossing locations were generally associated with high-probability crossing zones supports the use of model outputs by highway planners to evaluate potential crossing zones in western Colorado.

Species with high adjacency to transportation corridors have a heightened vulnerability to vehicle-related mortality compared to those with considerable spatial separation. The high frequency at which lynx crossed highways suggests that risk of vehicle-related mortality was high, which in turn justifies appropriate highway mitigation. Model results at the landscape scale indicate that mitigation actions that promote forest cover immediately adjacent to highways may increase permeability by lynx, especially on north-facing slopes and in drainage bottoms. In addition, the diel crossing pattern of lynx suggests that lower nighttime speed limits on highways in lynx habitat may decrease collision mortality. These suggested mitigation measures are based on resident lynx in winter-spring home ranges that contain highways; we did not directly investigate movements of dispersers or individuals making long distance movements from established territories. Thus, we acknowledge that transient or dispersing felids, or those engaging in exploratory movements, may cross highways where few predictive factors occur (Tewes & Hughes, 2001); these lynx may be more susceptible to vehicle collision than resident animals due to unfamiliar terrain (Beier, 1995; Ferreras et al., 1992).

Physical crossing structures, such as over/under passes and fencing, effectively facilitate safe wildlife crossings of major highways (Foster & Humphrey, 1995; Ng, Dole, Sauvajot, Riley, & Valone, 2004; Yanes, Velasco, & Suárez, 1995). However, the extent to which these improvements benefit lynx may depend on size of the highway and related traffic volume, as well as the landscape structures around the passes. Our GPS locations at 20 min intervals were inadequate to provide detailed depictions of how lynx responded to physical highway structures, like guard rails and cul-

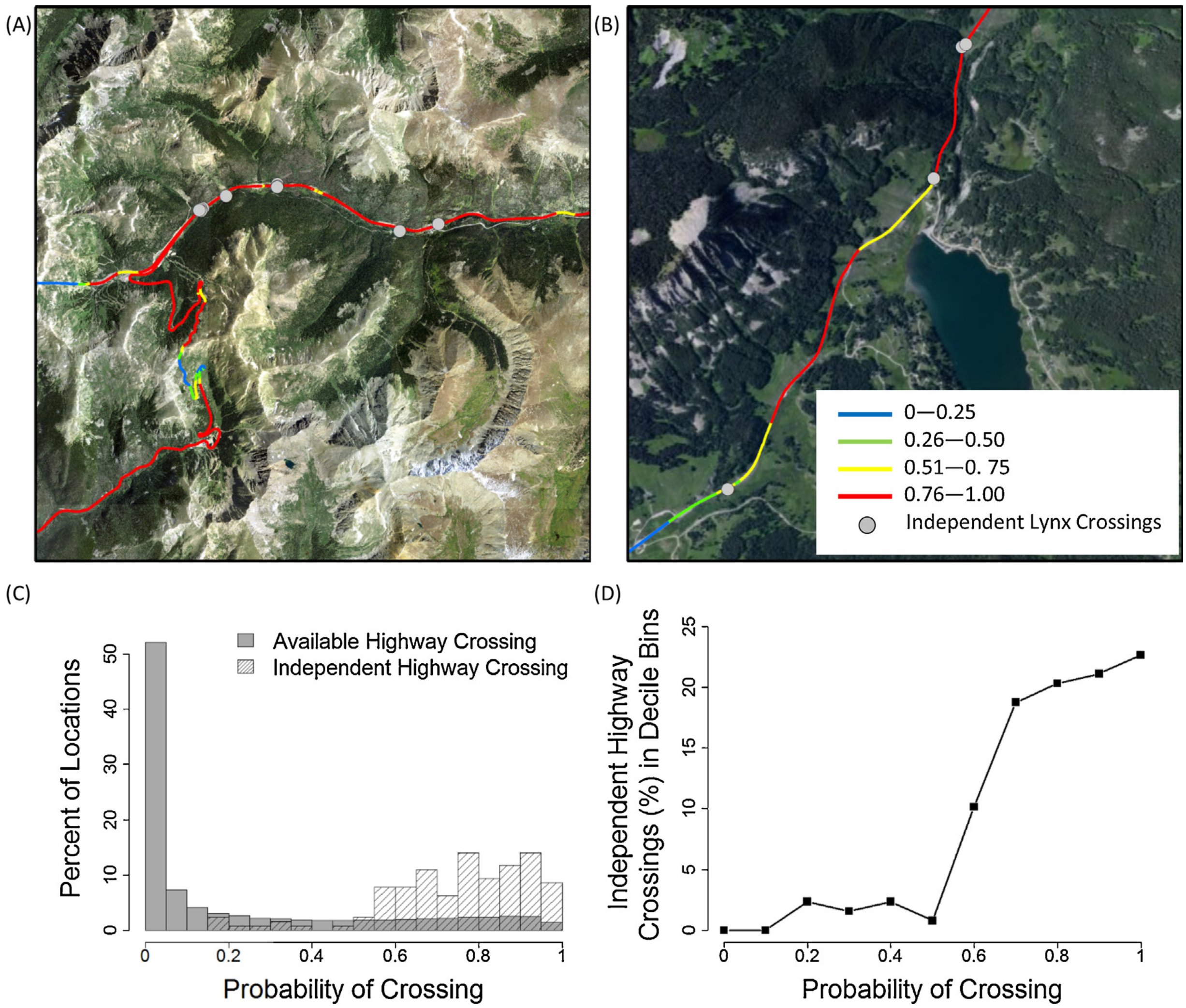



**Fig. 6.** Examples of the predicted resource selection function surface showing the probability of Canada lynx crossing a highway compared to independent known crossing locations (snowtracking and vehicle-related mortalities; indicated by gray dot) in western Colorado (panels A, B). Panel C shows distribution of predicted probabilities of crossing at all available locations in the landscape-scale RSF versus actual probabilities at independent crossing locations; independent crossings occurred with increasing frequency within the top deciles of binned crossing probabilities (panel D).

verts. In future studies, collars with greater temporal resolution, such as 10 or even 5 min intervals, might be more successful in documenting animal movement relative to highway structures at a fine spatial and temporal scale. However, the broad spatial distribution and sheer number of highway crossings that we documented indicate that lynx mostly crossed two-lane highways at road grade, and they did not depend on physical highway improvements to traverse two-lane highways. Similarly, Tigas et al. (2002) reported a preference by bobcats to cross highways at the surface and Crooks et al. (2008) failed to detect lynx using any of seven underpasses that were constructed specifically to reduce lynx highway mortalities in Colorado.

Our anecdotal observations of lynx crossing I-70, a high traffic four-lane divided highway, suggested that resident lynx did locate safe, below-grade crossings at large underpasses and used them repeatedly. They were also capable of crossing I-70 at road-grade during periods of low traffic volume. The use of underpasses for crossing high volume roads was consistent with other studies. For example, Beier (1995) observed numerous cougars crossing underneath major highway bridges over watercourses and Henke, Cawood-Hellmund, and Sprunk (2001) showed that several mammalian species in Colorado, including bobcats, used below grade highway crossings on major interstate highways. We assume lynx cross high-volume, four-lane highways similar to other wildlife in their proclivity to use larger underpasses with dense native vegetation close to passage entrances (Cain et al., 2003) in favorable habitat with low human disturbance (Beier, 1995; Ng et al., 2004).

## 5. Conclusions

We demonstrated that, at a fine scale, lynx crossed two-lane highways in forests with higher tree basal area and lower distance to cover. At the landscape scale, lynx selected highway crossings in areas of high forest canopy cover, especially in drainages and on north-facing slopes. The presence of highway infrastructure (guard rails and barriers) was not predictive of crossing two-lane highways. Model results indicated considerable individual variation in crossing behavior and the presence of multiple crossing zones within home ranges when bisected by extensive highway sections. Thus, appropriate mitigation to enhance connectivity for Canada lynx across 2-lane highways may include reduced speed limits at night and vegetation management rather than intensive investments for physical overpasses in few putative crossing zones. However, our anecdotal observations ($n = 25$ crossings) of lynx crossing a high-volume four-lane highway (I-70) suggest that investment in large elevated underpasses across drainages, especially in highway sections with forested medians, may be warranted.

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## Appendix A. Candidate RSF models

Candidate fine- and landscape-scale resource selection function models considered to predict Canada lynx highway crossing locations in western Colorado.

| Scale | Model # | Model Structure |
|---|---|---|
| Fine Scale Models | 1 | AvgDistCover |
| | 2 | MaxDistCover |
| | 3 | AvgBasalArea |
| | 4 | AvgHorizCover |
| | 5 | MinHorizCover |
| | 6 | MaxDistCover + AvgBasalArea |
| | 7 | MaxDistCover + AvgBasalArea + AvgHorizCover |
| | 8 | MaxDistCover + AvgBasalArea + AvgHorizCover + PropSF |
| | 9 | MaxDistCover + AvgBasalArea + PropSF |
| | 10 | AvgDistCover + AvgHorizCover |
| | 11 | AvgBasalArea + AvgHorizCover |
| | 12 | AvgBasalArea + AvgHorizCover + PropSF |
| | 13 | Null |
| Broad Scale Models | 1 | MEANBRT500 |
| | 2 | MEANWET200 + MEANBRT500 |
| | 3 | MEANWET200 + MEANBRT500 + STDBRT500 |
| | 4 | MEANBRT500 + STDBRT500 |
| | 5 | LFCNCVR500 |
| | 6 | MEANWET200 + LFCNCVR500 |
| | 7 | MEANWET200 + NDVI200 + LFCNCVR500 |
| | 8 | NDVI200 + STDBRT500 + LFCNCVR500 |
| | 9 | MEANBRT500 + PCTNRTH200 |
| | 10 | MEANBRT500 + TPI1000 |
| | 11 | MEANBRT500 + TPI1000 + PCTNRTH200 |
| | 12 | MEANBRT500 + ROUGH500 |
| | 13 | MEANBRT500 + MEANSLP500 |
| | 14 | MEANWET200 + MEANBRT500 + PCTNRTH200 |
| | 15 | MEANWET200 + MEANBRT500 + TPI1000 |
| | 16 | MEANWET200 + MEANBRT500 + TPI1000 + PCTNRTH200 |
| | 17 | MEANWET200 + MEANBRT500 + ROUGH500 |
| | 18 | MEANWET200 + MEANSLP500 |
| | 19 | MEANBRT500 + STDBRT500 + PCTNRTH200 |
| | 20 | MEANBRT500 + STDBRT500 + TPI1000 |
| | 21 | MEANBRT500 + STDBRT500 + TPI1000 + PCTNRTH200 |
| | 22 | MEANBRT500 + STDBRT500 + ROUGH500 |
| | 23 | MEANBRT500 + STDBRT500 + MEANSLP500 |
| | 24 | LFCNCVR500 + PCTNRTH200 |
| | 25 | LFCNCVR500 + TPI1000 |
| | 26 | LFCNCVR500 + TPI1000 + PCTNRTH200 |
| | 27 | MEANWET200 + LFCNCVR500 + PCTNRTH200 |
| | 28 | MEANWET200 + LFCNCVR500 + TPI000 |
| | 29 | NDVI200 + STDBRT500 + LFCNCVR500 + TPI1000 |

## Appendix B. Predictor variables

*Table B1*

Variables aggregated from eight vegetation plots and three roadside sample points at used and available lynx highway crossing points, used to evaluate fine scale resource selection functions predicting Canada lynx highway crossing locations in western Colorado.

| Type | Variable Name | Description |
|---|---|---|
| Vegetation Plots | PropSpruceFir | Percentage of "In" trees on plots that were Engelmann spruce or Subalpine fir. |
| | AvgBasalArea | Average basal area (sq. meters/ha) of plots, measured with a 10-BAF prism. |
| | MaxBasalArea | Maximum basal area among plots, measured with a 10-BAF prism. |
| | AvgHorizCover | Mean horizontal cover of plots. |
| | MinHorizCover | Minimum horizontal cover among plots. |
| | AvgPlotSlope | Average slope (%) of plots. |
| | MaxPlotSlope | Maximum slope (%) among plots. |
| | PctTreesLess | Percentage of "In" trees on plots with diameter <5". |
| | PctTreesGE5Less9 | Percentage of "In" trees on plots with diameter $\geq$5 and <9". |
| | PctTreesGE9Less20 | Percentage of "In" trees on plots with diameter $\geq$9 and <20". |
| | PctTreesGE20 | Percentage of "In" trees on plots with diameter $\geq$20". |
| Roadside Sample Plots | AvgRoadSlope | Average roadside slope (%) at sample points. |
| | MaxRoadSlope | Maximum roadside slope (%) among sample points. |
| | AvgRoadVisibility | Average distance of continuous pavement visible from sample points. |
| | AvgDistCover | Average distance from sample points to the nearest stand of continuous trees or shrubs >2 m tall and $\geq$25 $m^2$. |
| | MaxDistCover | Maximum distance among sample points to the nearest stand of vegetation >2 m tall and $\geq$25 $m^2$. |
| | MinDistCover | Minimum distance among sample points to the nearest stand of vegetation >2 m tall and $\geq$25 $m^2$. |
| | RoadCliff | Tally of vertical roadside cliffs >5 m high within 25 m of sample points |
| | RoadManBarrier | Tally of man-made structures, including guard rails and jersey barriers, within 25 m of sample points. |

*Table B2*

Variables extracted from GIS at used and available lynx highway crossings and used to evaluate landscape scale resource selection functions to predict Canada lynx highway crossing locations in western Colorado. Variables were calculated at two spatial scales: within a 200 or 500 m buffer around each crossing point.

| Type | Variable Name | Description |
|---|---|---|
| Topography | MEANSLOPE | Average slope (%) from a 10 m digital elevation model. |
| | ROUGH | An index of terrain roughness, calculated as the standard deviation (SD) of elevations. |
| | PCTNORTH | Percentage of area composed of north-facing aspects (>270° and <90°) for slopes >10%. |
| | TPI | Relative topographic position index, where negative values represent topographic concavities and positive values represent ridges. |
| | DISTHYDRO | Average distance to the nearest 14th-level (HUC) national hydrography dataset stream or waterbody. |
| Vegetation | LFCANCVR | Average of LANDFIRE canopy cover values, expressed as a percentage. |
| | NDVI | Average Normalized Difference Vegetation Index values derived from Landsat 5 TM images. |
| | MEANBRT | Average spectral variations in soil background reflectance (Brightness) derived from a Tasseled Cap transformation of Landsat 5 TM images. |
| | STDBRT | Standard deviation of spectral variations in soil background reflectance (Brightness) derived from a Tasseled Cap transformation of Landsat 5 TM images. |
| | MEANGRN | Average spectral variations in the vigor of green vegetation (Greenness) derived from a Tasseled Cap transformation of Landsat 5 TM images. |
| | STDGRN | Standard deviation of spectral variations in the vigor of green vegetation (Greenness) derived from a Tasseled Cap transformation of Landsat 5 TM images. |
| | MEANWET | Average spectral variations related to canopy and soil moisture (Wetness) derived from a Tasseled Cap transformation of Landsat 5 TM images. |
| | STDWET | Standard deviation of spectral variations related to canopy and soil moisture (Wetness) derived from a Tasseled Cap transformation of Landsat 5 TM images. |
| | MEANPCA1 | Average of values from the first Principal Component transformation of Landsat 5 TM image band ratios, which generally correspond to image brightness. |
| | MEANPCA2 | Average of values from the second Principal Component transformation of Landsat 5 TM image band ratios, which generally describes variations in vegetation cover. |

## Appendix C. Lynx Highway Crossing Summary

*Table C1*

Summary information for each Canada lynx used to assess highway crossing avoidance within a home range in western Colorado, 2010–2012. Columns show the lynx ID, sex, start and end date of collaring, number of days the animal was collared, number of GPS points collected during this time, percent of GPS fix attempts that were successful, number of road crossings exhibited during this time, number of crossings per day, mean number of crossings as simulated by correlated random walk (Avg Sim Cross), and the non-parametric p-value from the comparison of actual crossings against the simulated distribution. Bold values indicate significantly fewer crossings than expected by chance at $\alpha = 0.05$.

| Lynx | Sex | Start Date | End Date | # Days | # Points | % Success | # Cross | Cross/Day | Avg Sim Cross | p-value |
|---|---|---|---|---|---|---|---|---|---|---|
| F02 | F | 16-Mar-10 | 16-Apr-10 | 31 | 1925 | 86 | 24 | 0.77 | 64 | 0.01 |
| F03 | F | 28-Feb-12 | 31-May-12 | 92 | 5602 | 85 | 62 | 0.67 | 61 | 0.52 |
| M01 | M | 19-Feb-12 | 31-May-12 | 101 | 6730 | 93 | 68 | 0.67 | 88 | 0.35 |
| F04 | F | 22-Mar-10 | 10-Apr-10 | 19 | 1096 | 80 | 6 | 0.32 | 19 | 0.13 |
| M02 | M | 11-Mar-11 | 14-Apr-11 | 34 | 752 | 92 | 9 | 0.26 | 79 | **0.01** |
| F06 | F | 22-Feb-12 | 31-May-12 | 98 | 5693 | 81 | 33 | 0.34 | 114 | **0.04** |
| M04 | M | 25-Feb-12 | 31-May-12 | 95 | 6510 | 95 | 105 | 1.11 | 142 | 0.17 |
| F07 | F | 27-Jan-12 | 17-Jun-12 | 141 | 8300 | 82 | 106 | 0.75 | 221 | **0.02** |
| M05 | M | 12-Feb-12 | 31-May-12 | 108 | 7399 | 95 | 148 | 1.37 | 184 | 0.21 |
| M06 | M | 18-Feb-12 | 31-May-12 | 102 | 6658 | 91 | 27 | 0.26 | 53 | 0.29 |
| M07 | M | 28-Feb-12 | 31-May-12 | 92 | 5883 | 89 | 19 | 0.21 | 41 | 0.24 |
| M08 | M | 17-Feb-11 | 14-Jun-11 | 117 | 2611 | 93 | 29 | 0.25 | 71 | **0.01** |
| F08 | F | 5-Feb-11 | 15-Jun-11 | 130 | 2890 | 93 | 11 | 0.0 | 32 | 0.07 |

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